

AN ASSESSMENT OF REBUILDING TIMES FOR GOLIATH GROUPER



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Introduction

The goliath grouper, *Epinephelus itajara*, is the largest grouper in the western North Atlantic and one of the largest in the world (Sadovy and Eklund 1999). This species grows to approximately 2 meters and lives to at least 37 years (Bullock et al. 1992). It reaches reproductive maturity at a large size (one meter) and late age (4-7 years). This life history strategy, along with a curious and unwary behavior, make it highly vulnerable to overexploitation (Sadovy and Eklund 1999). Its range includes both sides of the Atlantic Ocean and along the coast of Mexico in the eastern Pacific, although it may have been extirpated from that area. Along the western Atlantic, the species ranges from the Carolinas, into the Gulf of Mexico, the Caribbean and down the coast of Brazil (Sadovy and Eklund 1999).

The Gulf of Mexico and the South Atlantic Fishery Management Councils closed the fishery for goliath grouper in 1990, by emergency rule, due to concerns of overfishing. The Caribbean Fishery Management Council followed by closing the fishery in 1993. No harvest has been allowed in federal waters since that time. A SEDAR data workshop¹ was convened in early 2003 to examine the data available for determining the status of the goliath grouper stock. During the meeting, several fishermen reported that goliath grouper sales had often been to buyers other than dealers (dealers are the source of federal commercial landings statistics) and that the proportion of the catch sold through dealers may have changed over time. Based on this testimony, the SEDAR participants concluded that the catch statistics were unreliable and that a meaningful assessment was not possible for goliath grouper.

Most stock assessment approaches do indeed require reliable catch data, however a number of *ad hoc* methods have been developed to accommodate 'data-poor' situations. For example, an approach that is often taken when research surveys or other indices of abundance are available is to set the minimum stock size threshold (MSST) equal to some fraction of the survey values observed during an earlier portion of the time series when the stock was presumably close to pre-exploitation or MSY levels. Such 'model free' approaches have the advantage of assuming relatively little about the recovery rate of the stock, but cannot be used to estimate many of the reference points stipulated by the Magnuson-Stevens Act. Moreover, there may be other types of information about the fishery that could influence the perception of the status of the stock and it would be useful to integrate that information formally into the assessment.

The purpose of this paper is to assess the status of the goliath grouper stock in U.S. waters (principally southern Florida) by use of an estimation framework developed specifically for data-poor situations. The model recasts the canonical age-structured equations in terms relative to pre-exploitation levels, thus eliminating the need for catch information. A Bayesian estimation scheme is adopted to allow the incorporation of pertinent auxiliary information such as might be obtained from meta-analyses of similar stocks or anecdotal observations.

¹Anon. SEDAR Goliath Grouper Data Workshop Report, March 2003. 11 pp.

Methods

Population dynamics

The stock was assumed to be near virgin levels in 1950, such that the relative abundance N of each age class a at the beginning of 1950 is given by

$$(1) \quad N_{a,1950} = \begin{cases} 1 & \{\text{for } a = a_r\} \\ N_{a-1,1950} e^{-M_a} & \{\text{for } a_r < a \leq A\} \end{cases}.$$

where a_r is the age when the animal first recruits to the fishery, A is the maximum age attainable, and M is the natural mortality rate. The relative abundance at the beginning of subsequent years (y) is modeled by the recursion

$$(2) \quad N_{a,y} = \begin{cases} r_y = \Psi(s_{y-a_r}) e^{e_y} & (a = a_r) \\ N_{a-1,y-1} e^{-F_{y-1} v_{a-1} - M_{a-1}} & (a_r < a \leq A) \end{cases}$$

$$s_y = \frac{\sum_{a=a_r}^A E_a e^{-(F_y v_a + M_a) t_s} N_{a,y}}{\sum_{a=a_r}^A E_a e^{-M_a t_s} N_{a,1}}$$

The vector v represents the relative vulnerability of each age class to the fishery, which implicitly includes factors such as gear selectivity, size limit regulations, and the fraction of the stock exposed to the fishery. The variable F represents the fishing mortality rate on the most vulnerable age class. In this regard the model distinguishes three time periods: a ‘historical’ period (1950-1979) during which the fishing mortality rate is assumed to have increased linearly through time, a ‘modern’ period (1980-1989) when the fishing mortality rate was relatively constant, and a ‘moratorium’ period (1990 onwards) during which the fishing mortality rate is assumed to be negligible.

The variable r is the recruitment relative to virgin levels expressed as a function Ψ of the spawning stock relative to virgin levels s , which in turn is expressed as a function of an index of the per-capita number of eggs produced by each age class (E) and the fraction of the year elapsed at the time of spawning (t_s). In this case Ψ is assumed to be of the Beverton and Holt type expressed in terms of the maximum lifetime reproductive rate α (see derivation in Appendix 1):

$$(3) \quad \Psi(s) = \begin{cases} s \alpha^{1-s} & \text{Ricker} \\ \frac{\alpha s}{(1 + s(\alpha - 1))} & \text{Beverton and Holt} \end{cases}$$

The shapes of these two curves are essentially the same as the conventional Ricker or Beverton and Holt relationships, however their domain is implicitly limited to the interval $0 \leq s \leq 1$. Deviations in recruitment (e_y) from the expectation $\Psi(s)$, ostensibly due to fluctuations in the environment, are

modeled as a first-order, lognormal autoregressive process,

$$(4) \quad \begin{aligned} r_y &= \Psi(s_{y-a}) e^{\mathbf{e}_y} \\ \mathbf{e}_y &= \mathbf{r}\mathbf{e}_{y-1} + \mathbf{h}_y \end{aligned} ,$$

where \mathbf{r} is the correlation coefficient (here 0.5) and \mathbf{h} is a normal-distributed random variate having mean 0 and standard deviation σ_r (here 0.4 on a log-scale).

Reference points

The set of equations 1-4 describe the relative dynamics of a population apart from its absolute abundance. As such they are most suited for developing management plans where the fishing mortality rate is controlled directly (e.g., by reducing effort) and the biomass reference points are expressed on a relative scale. When the virgin spawning biomass itself is used as the reference point, the estimated value of s_y is a direct measure of the status of the stock. For example, if the management goal is to maintain spawning biomass at or above 50% of the virgin level, then estimates of s below 0.5 might trigger some action to reduce fishing pressure.

A related reference point is the equilibrium spawning potential ratio (Goodyear, 1993), defined as the expected lifetime fecundity per recruit at a given F (\mathbf{f}_F) divided by the expected lifetime fecundity (maximum spawning potential) in the absence of fishing (\mathbf{f}_0):

$$(5) \quad p = \frac{\mathbf{f}_F}{\mathbf{f}_0}$$

$$\mathbf{f}_F = \sum_{a=0}^A E_a e^{-(F_a + M_a)t_s} e^{-\sum_{i=0}^{a-1} Fv_i + M_i}$$

where E is relative egg production by each age class and t_s is the time of spawning. As shown in Appendix 2, the corresponding equilibrium spawning biomass (relative to the virgin level) may be computed as

$$(6) \quad \tilde{s}_p = \begin{cases} 1 + \frac{\log_e p}{\log_e a} & \text{Ricker} \\ \frac{ap - 1}{a - 1} & \text{Beverton and Holt} \end{cases} .$$

Thus, management actions may be triggered when the estimates of s fall below the estimate of \tilde{s}_p .

Other management plans employ reference points such as F_{max} or $F_{0.1}$, which are based on the

yield per recruit statistic

$$(7) \quad \left(\frac{Y}{R} \right) = \sum_{a=0}^A w_a F v_a \frac{1 - e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i},$$

where w_a is some measure related to the average weight of the catch. Inasmuch as there are no terms involving the absolute abundance of the stock, the calculation of such statistics poses no special problems for the relative framework presented here. The corresponding values of p (and therefore \tilde{s}_p) may be calculated via equation (5).

Prescriptions based on maximum sustainable yield (*MSY*) are slightly more complicated because equilibrium yield is the product of equilibrium recruitment \tilde{R} and equilibrium yield per recruit:

$$(8) \quad \tilde{Y} = \tilde{R}_F \sum_{a=0}^A w_a F v_a \frac{1 - e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i},$$

However, the fishing mortality rate that maximizes (8) also maximizes (8) divided by the virgin recruitment R_0 (a constant). Thus, F_{MSY} may be obtained from

$$(9) \quad \max_F \left\{ \frac{F \tilde{s}_p}{p} \sum_{a=0}^A w_a v_a \frac{1 - e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i} \right\}.$$

where \tilde{s}_p / p has been substituted for \tilde{R} / R_0 (from equation A.4 in Appendix 1). Inasmuch as the absolute abundance is not estimable, the absolute value of *MSY* may not be calculated directly.

Bayesian estimation

The equations above include numerous ‘unknowns’ representing the processes of reproduction, mortality and growth. In the case of “data-poor” stocks like Goliath grouper, there are insufficient data to estimate all of these unknown parameters with an acceptable level of precision. However, it is often possible to increase the precision of the estimates through the use of Bayesian prior probability densities constructed to reflect anecdotal information or the results from meta-analyses involving similar species (Gelman et al. 1995, Liermann and Hilborn 1997).

The Bayesian approach to estimation seeks to develop a ‘posterior’ probability density for the parameters Q that is conditioned on the data D , $P(Q | D)$. By application of Bayes rule it is easy to show that

$$(10) \quad P(\Theta | D) \propto P(D | \Theta) P(\Theta).$$

where $P(D | Q)$ is the sampling density (likelihood function) and $P(Q)$ is the prior density (the analyst’s best guess of the probability density for Q). Estimates for Q may be obtained from (9) by integrating the posterior (classical Bayes moment estimator)

$$(11) \quad \hat{q}_i = \int q_i P(D | \Theta) P(\Theta) dq_i, \quad q_i \in \Theta.$$

or by minimizing its negative logarithm (highest posterior density estimator)

$$(12) \quad \min_{\Theta} \{-\log_e P(D | \Theta) - \log_e P(\Theta)\} .$$

In the present model, a prior needs to be specified for the parameters reflecting recruitment (α , ρ , \mathbf{s}_r and \mathbf{e}), mortality (M , F , ν), fecundity (E) and growth in weight (w). It is here assumed that the parameters are statistically independent with respect to prior knowledge such that the joint prior is merely the product of the marginal priors for each parameter. The lone exceptions are the parameters for the annual recruitment deviations \mathbf{e}_y , which are assumed to be autocorrelated lognormal variates such that

$$(13) \quad -\log P(\mathbf{e}) = \frac{1}{2\mathbf{s}_r^2} \left[\mathbf{e}_1^2 + \sum_{y=1}^{w-1} (\mathbf{e}_{y+1} - \mathbf{r}\mathbf{e}_y)^2 \right] + w \log \mathbf{s}_r$$

where w is the last year in the simulation, \mathbf{r}_r is the correlation coefficient (here 0.5) and \mathbf{s}_r^2 is the variance of $\log \mathbf{h}$ (for stability reasons, it is assumed that $\mathbf{e}_0 = 0$).

It is possible, at least in principle, to conduct an assessment based on prior specifications alone. However, it may be difficult to develop sufficiently informative priors for some of the parameters, particularly the fishing mortality rates. The preferred approach is to condition the estimates on data. For example, visual counts of goliath grouper have been conducted at several fixed locations since 1982. To the extent that changes in the abundance at these locations (n) are proportional to changes in the abundance of the population as a whole (N), the visual counts (c) may be modeled as:

$$(14) \quad c_{i,y} = q_i \sum_a v_{i,a} N_{a,y} e^{-(F_y v_a + M_a)t_i} e^{\mathbf{x}_{i,y}} .$$

$$\mathbf{x}_{i,y} \sim \text{Normal}(0, \mathbf{s}_i)$$

where i indexes the location, q is the proportionality coefficient scaling the number counted to the relative abundance of the population, $v_{i,a}$ is the relative vulnerability (availability) of each age class at the survey site, t_i is the fraction of the year elapsed at the time of the survey, and \mathbf{s}_i is the standard deviation of the fluctuations in $\log_e c_i$ owing to observation errors or changes in the distribution of the stock. The corresponding negative logarithm of the sampling density is

$$(15) \quad -\log P(c|\Theta) = \sum_y \left\{ \frac{1}{2\mathbf{s}_i^2} (\log_e c_{i,y} - q_i \sum_a v_{i,a} N_{a,y} e^{-(F_y v_a + M_a)t_i})^2 + \log \mathbf{s}_i \right\}$$

An alternative to the use of data is to construct priors relating to auxiliary information such as anecdotal perceptions of the abundance of the resource relative to virgin levels (n). In such cases an appropriate model might be

$$(16) \quad n_y = \frac{\sum_a I_a N_{a,y} e^{-(F_y v_{i,a} + M_a) d}}{\sum_a I_a e^{-M_a d} e^{-\sum_{i=0}^{a-1} M_i}} e^{z_y}$$

$$z_{i,y} \sim Normal(0, s_n)$$

where $I_{.a}$ is the relative contribution of each age class in forming the perception of total abundance (e.g., fishermen may never encounter very young fish), d is the time of the year most reflective of the period upon which the perceptions were based (e.g., the peak of the fishing season), and s_n is the standard deviation of the fluctuations in $\log_e n_y$ owing to errors in perception. Note that such auxiliary priors are mathematically equivalent to sampling densities and we do not here distinguish between them.

The model was implemented using the nonlinear optimization package AD Model Builder (Otter Research Ltd.²), which provides facilities for estimating the mode and shape of the posterior distribution (equation 10).

Application to goliath grouper

The retention of goliath grouper is currently prohibited by law, but status determination criteria have not been defined nor has the duration of the moratorium been specified. The Caribbean Fishery Management Council (CFMC, 2001) postulated that the biomass of the populations under their jurisdiction were so much lower than any reasonable MSST that recovery would be unlikely to occur within 10 years. They therefore set the allowable rebuilding period equal to 10 years plus one generation time, where the generation times were estimated by Legault and Eklund³ to be between 15 to 40 years for goliath grouper. The CFMC preferred the lower end of the range because it is more ‘precautionary’ in the sense that managers are under greater compunction to prohibit harvest when they are constrained to rebuild over a short time frame.

Natural mortality

Legault and Eklund² developed estimates for M ranging from 0.04 to 0.19 for goliath grouper based on its perceived life spans. Estimates from Hoenig’s (1984) method based on a maximum observed age of 37 years (Sadovy and Eklund 1999) suggests an expected value of 0.11. An examination of the range of plausible values from Legault and Eklund² suggested a lognormal prior with median 0.11 and CV about 0.4.

²Otter Research Ltd. 2001. An introduction to AD MODEL BUILDER Version 4.5. Box 2040, Sidney B.C. V8L 3S3, Canada. 141 p.

³Legault, C.M. and Eklund, A.-M. 1998. Generation times for Nassau grouper and jewfish with comments on M/K ratios. Sustainable Fisheries Division Contribution SFD-97/98-10A. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.

Stock-recruitment relationship

As far as we are aware, there is no reliable information on the nature of the spawner-recruit relationship for any goliath grouper populations (or, for that matter, any subtropical serranid). Myers et al (1999) examined over 700 spawner-recruit series (none of them serranids) with a broad spectrum of a values ranging between 1.4 and 123.5. Rose et al. (2000), however, have subdivided this data set according to three general life history strategies: opportunistic, periodic and equilibrium. Of these, the ‘periodic’ strategy (larger, highly fecund fishes with long life spans) appears most descriptive of Goliath grouper. Accordingly, we developed a prior for a by fitting a lognormal distribution to the frequency histogram of values corresponding to the periodic strategists represented in the Myers et al (1999) data set (Figure 1).

Fecundity and growth

To date there are insufficient data for estimating a fecundity-at-age relationship. We follow Legault and Eklund² and substitute the weight at age relationship:

$$(17) \quad E_a = \begin{cases} 0 & a < 6 \\ w_a = 1.31 \times 10^{-5} l^{3.056} & a \geq 6 \end{cases},$$
$$l = 200.6(1 - e^{-0.126(a + 0.49)})$$

where w is weight in kg and l is length in cm expressed as a von Bertalanffy function of age (see Bullock et al., 1992). Uncertainty in these parameters was reflected by imposing a normal prior on the asymptotic length with a 6% CV and a lognormal prior on k with log-scale variance equal to 0.204.

Historical vulnerability to fisheries

There is little quantitative information on the vulnerability (v) of goliath groupers to the fishery that existed prior to the moratorium. A large fraction of the recreational landings of goliath grouper appear to have been from the ten thousand islands area, where most of the animals observed to date are between the ages of one and four. However, large animals were often targeted by commercial and recreational fishers in other areas. Thus it is unclear how the overall vulnerability of goliath grouper changes with age. We assume the vulnerability of goliath grouper generally increased with age according to the sigmoid-shaped logistic curve:

$$(18) \quad v_a = \frac{1}{1 + e^{-(a - a_{50})/d}}$$

where a_{50} is the age of 50% relative vulnerability for fleet and d is the dispersion coefficient controlling the slope of the curve at a_{50} (values of d less than 0.2 effectively imply knife-edge selection). In order to estimate the parameters a_{50} and d , we converted length composition data

collected during the course of a creel survey in the Ten Thousand Islands area (courtesy T. Schmidt⁴) into age composition data by use of an age-length key derived from experimental trap and trot-line catches (Brusher and Schull⁵). We then fitted a logistic vulnerability curve (weighted by cumulative mortality) to the observed frequency of ages 0 to 5 (older age classes appear to migrate out of the area but are caught elsewhere). The estimated values of $a_{50\%}$ and d are 2.51 and 0.525, respectively (see Figure 2). Uncertainty was incorporated via normal priors on $a_{50\%}$ with 10% CV's.

Survey information

Porch and Eklund (2003) have developed relative indices of abundance from two visual surveys: the personal observations of a professional spearfisher (DeMaria⁶) and a volunteer fish-monitoring program administered by the Reef Education and Environmental Foundation (REEF 2000). In addition, Cass-Calay and Schmidt (2003) have standardized catch rate data collected in the Ten Thousand Islands area by the Everglades National Park (ENP). We assume the two visual surveys reflect the abundance of ages 6 and older and that the ENP index reflects the relative abundance of ages 1 to 5 according to the dome-shaped gamma function (normalized to a maximum of 1):

$$(19) \quad v_a = \left(\frac{a}{a_{100\%}} e^{1-a/a_{100\%}} \right)^{g^{-2}-1}$$

where $a_{100\%}$ is the most vulnerable age and g is the coefficient of variation. Uncertainty was incorporated via a normal prior on $a_{100\%}$ with a 10% CV. Estimates for $a_{100\%}$ (3.47) and g (0.34) were obtained by fitting the cumulative mortality-weighted gamma curve to the frequency of ages 0 - 7 in age-converted ENP data described above (see Figure 2).

Anecdotal impressions of stock status

Johannes et al. (2000) point out that local fishers often disagree with the conclusions drawn by scientists in data-poor situations and that many times additional data will prove the fishers' correct. As mentioned earlier, expert judgements about the relative abundance of a stock can be treated as data and represented by a 'prior' (e.g., Punt and Walker, 1998; other examples). We developed a prior for the value of s at the time moratoriums began (1990) by interviewing fishers and divers who had been active in southern Florida during the 1960's or earlier (nine such individuals have so far been identified). Specifically, interviewees were asked to state their perception of the percent reduction in Goliath grouper populations from the time they began diving to the time the moratorium on catch was imposed (1990). The average percent reduction reported was 86% with a standard deviation of about 13%.

⁴Schmidt, T. W. Everglades National Park, U. S. National Park Service

⁵J. Brusher and J. Schull, in prep.

⁶DeMaria, Don. P.O. Box 420975, Summerland Key, FL 33042.

Results

The base model assumes the fishing mortality rate is nearly zero in 1950, increases linearly through 1979, is relatively constant between 1980 and 1989, and then drops off to near-zero from 1990 onwards owing to the moratorium. The model fit to the data is shown in Figure 3. As the Gulf of Mexico Fishery Management Council has recommended using benchmarks associated with an SPR of 50% as proxies for MSY benchmarks for Goliath grouper, statistics relative to this measure are reported herein. The estimated trends in spawning biomass relative to the equilibrium level corresponding to an SPR of 50% ($\tilde{s}_{50\%}$) and estimated fishing mortality rates are shown in Figure 4. The estimated probabilities that the population will have recovered to a level at or above $\tilde{s}_{50\%}$ are shown in Figure 5.

Numerous sensitivity runs were made examining (1) the effect of dropping one or more of the indices, (2) changing the youngest age assumed to be represented by the REEF and DeMaria indices from 6 to 10, (3) extending the historical period back to 1940, and (4) changing the years when the fishing mortality rate was assumed to be constant (1976-89 or 1984-89). None of these resulted in any substantial departure from the results presented in Figures 3-5 except when the ENP index was dropped from the analysis, in which case the estimated recovery rate was somewhat less optimistic (Figures 6 and 7).

An additional run was made allowing for large interannual deviations in F between 1980 and 1989 rather than assuming it was relatively constant (as might occur with fluctuations in demand and price) and allowing for moderate deviations in estimated recruitment from the Beverton and Holt relationship (as discussed in the methods section). The fit to the ENP index was substantially improved (Figure 8), but at the expense of highly imprecise estimates for F and s (Figure 9). The estimated probability distribution of the time of recovery derived from the posteriors for the relative biomass trend suggests that there is a 60% chance that the population has already recovered (Figure 10). However, we have little confidence that these probabilities are correct owing to the poor behavior of the solution surface. The likelihood profile routine used by ADMB crashed while calculating the posterior distributions for many of the parameters of interest and the posteriors calculated by the MCMC algorithm used by AD Model Builder were poorly behaved with modes that were sometimes quite different from the HPD estimates (even with 5,000,000 samples).

Discussion

One issue that merits further investigation is the choice of reference points. In the present paper we have adopted $\tilde{s}_{50\%}$, which is the equilibrium spawning biomass associated with a spawning potential ratio of 50% under the historical vulnerability pattern, as a proxy for the biomass at MSY. In the present framework, it also is possible to directly compute the equilibrium spawning biomass associated with MSY (\tilde{s}_{MSY}). Strictly speaking, this would be obtained by heavily exploiting a single optimal age class, but this is impossible to achieve for most stocks. The classical alternative is to define MSY as the maximum sustainable yield when the vulnerability is constant for all ages above some optimal age. In some cases, however, the definition of MSY is conditioned on the historical vulnerability pattern (which we will denote $MSY|v$). Reference points based on $MSY|v$ ($\tilde{s}_{MSY|v}$ and $F_{MSY|v}$) are often more risky than those based on classical approach because they are conditioned on fisher behavior. One can imagine, for example, a situation where fishers might focus on very young

juveniles for the live animal trade, in which case $\tilde{s}_{MSY|v}$ might be much lower than \tilde{s}_{MSY} and the stock more prone to collapse. Moreover, the reference points ($F_{MSY|v}$ and $\tilde{s}_{MSY|v}$, but $F_{MSY|v}$ moreso) have the unsettling tendency to change through time as fisher behavior changes, whereas \tilde{s}_{MSY} and F_{MSY} do not.

The $\tilde{s}_{50\%}$ proxy used here, like $\tilde{s}_{MSY|v}$, depends on the assumed historical vulnerability vector. The $MSY|v$ calculations, however, are likely to be doubly sensitive to mis-specifications of this vulnerability vector because the vulnerability vector is used to compute potential yield in addition to s . Inasmuch as the historical vulnerability of goliath grouper is poorly known, and apt to change if the fishery is reopened after more than a decade of closure, we recommend the $\tilde{s}_{50\%}$ proxy over $\tilde{s}_{MSY|v}$. If MSY -based measures are desired for reference points, then we recommend measures that are independent of fisher behavior such as the maximum sustainable yield under knife-edge selection after some optimal age.

We believe the best advice at present for managing the U.S. goliath grouper population should be predicated on the results of the base model (Figures 4 and 5). These indicate that there is about a 50% chance that the population will have recovered to $\tilde{s}_{50\%}$ by 2006 and about a 95% chance that it will recover by 2012. It is important to consider, however, that the three indices of abundance considered each focus on a relatively small portion of the potential range of goliath grouper (see Porch and Eklund 2003). It is believed that the center of abundance for the population in U.S. waters is southern Florida, particularly the Ten Thousand Islands area, but goliath grouper are known to have occurred throughout the coastal waters of Gulf of Mexico and along the east coast of Florida, and on up through the Carolinas. Inasmuch as goliath grouper are not highly migratory, it is possible it may take some additional time for the species to fully occupy its historical range, thus delaying the overall recovery of the stock.

There is perhaps some evidence of a delay in range expansion in a comparison of the REEF and DeMaria indices: The DeMaria index, which is based on sites adjacent to the Ten Thousand Islands area, indicates a noticeable recovery by 1994 while the REEF index, which is based on sites located along the southeast Florida Coast, indicates the increase began about 3 years later. However, it is also possible that the delay is attributable to the difference in habitat, the DeMaria index coming from isolated wreck sites and the REEF index coming from more continuous, natural reef habitats. Recent surveys (Eklund, pers. obs.) suggest that artificial reefs may be artificially concentrating goliath grouper and may not reflect their distribution and abundance on natural habitat. This concentration effect is well-known in artificial reef literature. In any case, we agree with the conclusions of the SEDAR stock assessment review panel⁷ that sampling throughout the geographic range would probably be important in ascertaining stock status, owing to the restricted home ranges and high site fidelity of these animals.

Somewhat less optimistic results were obtained when the ENP index was excluded from the analysis, in which case there is about a 50% chance that the population will have recovered to $\tilde{s}_{50\%}$ by 2008 and about an 80% chance that it will recover by 2012. Inasmuch as the ENP index is the

⁷ Anon. 2003. SEDAR Peer Review of Yellowtail Snapper Assessment, with comments on Goliath Grouper. Tampa, Florida. July 28-31, 2003. 12 pp.

longest and probably most representative time series, we feel it is inappropriate to exclude it in favor of the DeMaria index (based on only five sites) or REEF index (mostly based on sites along the fringes of the range of Goliath grouper). However, a caveat to keep in mind is that the ENP index is based on catch rate data, where declining trends are often somewhat masked by the ability of fishers to find local concentrations of fish. Moreover, the ENP data were collected from the Ten Thousand Islands area, where it is believed the species was the least impacted by changes in fishing pressure over time. Outside the Ten Thousand Islands, the decline in juvenile abundance may have been more rapid owing to increased fishing pressure as human population levels increased in southern Florida and recent technological advances (LORAN and GPS) that enabled fishers to consistently locate productive reefs and offshore wrecks. For these reasons, it may be that the historical decline in overall juvenile abundance was more precipitous than indicated by the ENP index. Within the context of the model, relatively flat trends in a juvenile index in concert with a dramatic increase in an adult index suggest a productive stock capable of rapid recovery. Thus, if the trends indicated by the ENP index are indeed flatter than for the overall juvenile population, then the base model results will likely be too optimistic.

The assessment herein also needs to be seen in light of the fact that the relationship between fecundity and age is unknown. We used weight-at-age as a proxy for the relative fecundity-at-age in our analysis, but it is often the case that fecundity increases with age faster than weight. If this is true for goliath grouper, then our projections would be too optimistic. Furthermore, although the results were not especially sensitive to our assumptions about the vulnerability coefficients for the REEF and DeMaria surveys, the same is not likely to be true of our assumptions about the vulnerability coefficients for the fishery. Information on the age composition of the historical catch is needed to estimate these coefficients, but at present none is available. There have been recent data collected on size estimates of goliath grouper on the sites used in the DeMaria index, and there may be some data mining through older video-surveys that may be available in the future.

Finally, we wish to reiterate that the methodology employed here cannot provide a direct estimate of the equilibrium catch level associated with any particular reference point such as MSY. This is because, in the absence of historical catch data, one is relegated to estimating the abundance of the stock relative to unexploited levels rather than absolute abundance. The situation could be ameliorated by obtaining estimates of absolute abundance from a comprehensive short-term survey covering the entire range of the animal. Alternatively, a long-term monitoring program at select sites located throughout the range could be established to detect changes in relative abundance under various closely monitored levels of catch.

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Appendix 1: Reparameterized spawner-recruit relationships

The number of young fish recruiting to a population is often related to the aggregate fecundity of the spawning stock using one of two functional forms:

$$(A.1) \quad R = \begin{cases} aSe^{-bS} & \text{Ricker} \\ \frac{abS}{b+S} & \text{Beverton and Holt} \end{cases} .$$

The parameter a is the slope of the curve at the origin and the parameter b controls the degree of density dependence. Notice that the domain of both functions extends from zero to infinity, whereas in practice there must be some limitation on S even in the absence of fishing owing to environmental constraints. This being so, we obtain

$$(A.2) \quad a \frac{S_0}{R_0} = \begin{cases} e^{bS_0} & \text{Ricker} \\ 1 + S_0/b & \text{Beverton and Holt} \end{cases}$$

The ratio S_0/R_0 represents the maximum expected lifetime fecundity of each recruit and a represents the survival of recruits in the absence of density dependence. Accordingly, the product $\mathbf{a} = aS_0/R_0$ may be interpreted as maximum possible number of spawners produced by each spawner over its lifetime (Myers et al. 1998).

The dimensionless character of \mathbf{a} makes it useful for interspecies comparisons, or for borrowing values from species with similar life history strategies. Solving for b in terms of \mathbf{a} one obtains

$$(A.3) \quad b = \begin{cases} \log_e \mathbf{a} / S_0 & \text{Ricker} \\ S_0 / (1 - \mathbf{a}) & \text{Beverton and Holt} \end{cases}$$

Substituting (A.3) into (A.1) gives

$$(A.4) \quad R = \begin{cases} aS\mathbf{a}^{-S/S_0} & \text{Ricker} \\ \frac{aS_0}{1 + (\mathbf{a} - 1)S/S_0} & \text{Beverton and Holt} \end{cases}$$

and, since $a = \mathbf{a}R_0/S_0$,

$$(A.5) \quad R = \begin{cases} R_0 \frac{S}{S_0} \mathbf{a}^{1-S/S_0} & \text{Ricker} \\ R_0 \frac{\mathbf{a}S/S_0}{1 + (\mathbf{a} - 1)S/S_0} & \text{Beverton and Holt} \end{cases}.$$

Dividing through by R_0 and defining $s = S/S_0$ gives equation (3).

Appendix 2: Formula for equilibrium spawning biomass

The spawning potential ratio (p) is defined as the number of spawners produced by each recruit at equilibrium with a given fishing mortality rate F divided by the number of spawners per recruit under virgin conditions ($F=0$). This may be written

$$(A.6) \quad p = \frac{f_F}{f_0} = \frac{\tilde{S}_F / \tilde{R}_F}{\tilde{S}_0 / \tilde{R}_0} = \frac{\tilde{S}_F / \tilde{S}_0}{\tilde{R}_F / \tilde{R}_0} = \tilde{s} / \tilde{r}$$

where the tilde signifies equilibrium values. At equilibrium we also obtain from equation (4)

$$(A.7) \quad \tilde{r} = \begin{cases} \tilde{s} \mathbf{a}^{1-\tilde{s}} & \text{Ricker} \\ \frac{\mathbf{a}\tilde{s}}{(1 + \tilde{s}(\mathbf{a} - 1))} & \text{Beverton and Holt} \end{cases}$$

Dividing both sides of (A.7) by \tilde{r} , substituting (A.6) and solving for \tilde{s} gives equation (6).

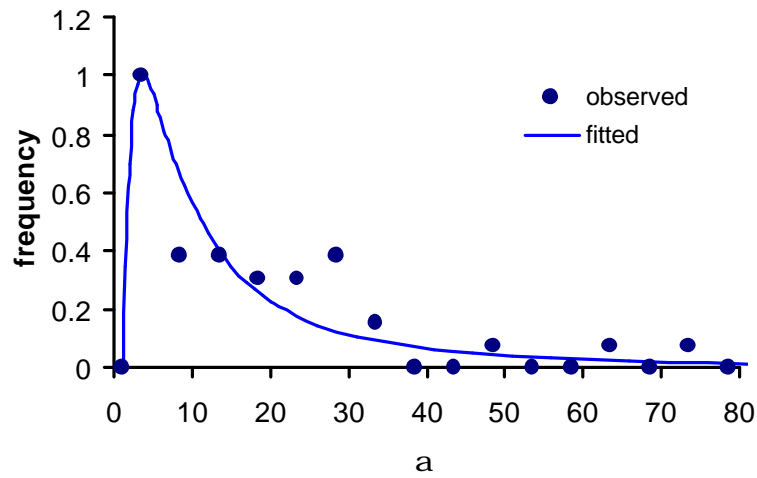


Figure 4. Prior for the maximum lifetime fecundity parameter (α), derived from the values in Myers et al. (1999) that correspond to species categorized as periodic strategists by Rose et al. (2000). The lognormal density was fitted to the values of $\alpha-1$ in Myers et al. (1999) corresponding to species classified as periodic strategists by Rose et al. (2000). The fitted distribution (with median 9.8 and log-scale variance 1.31) was then shifted 1 unit to provide a prior for α .

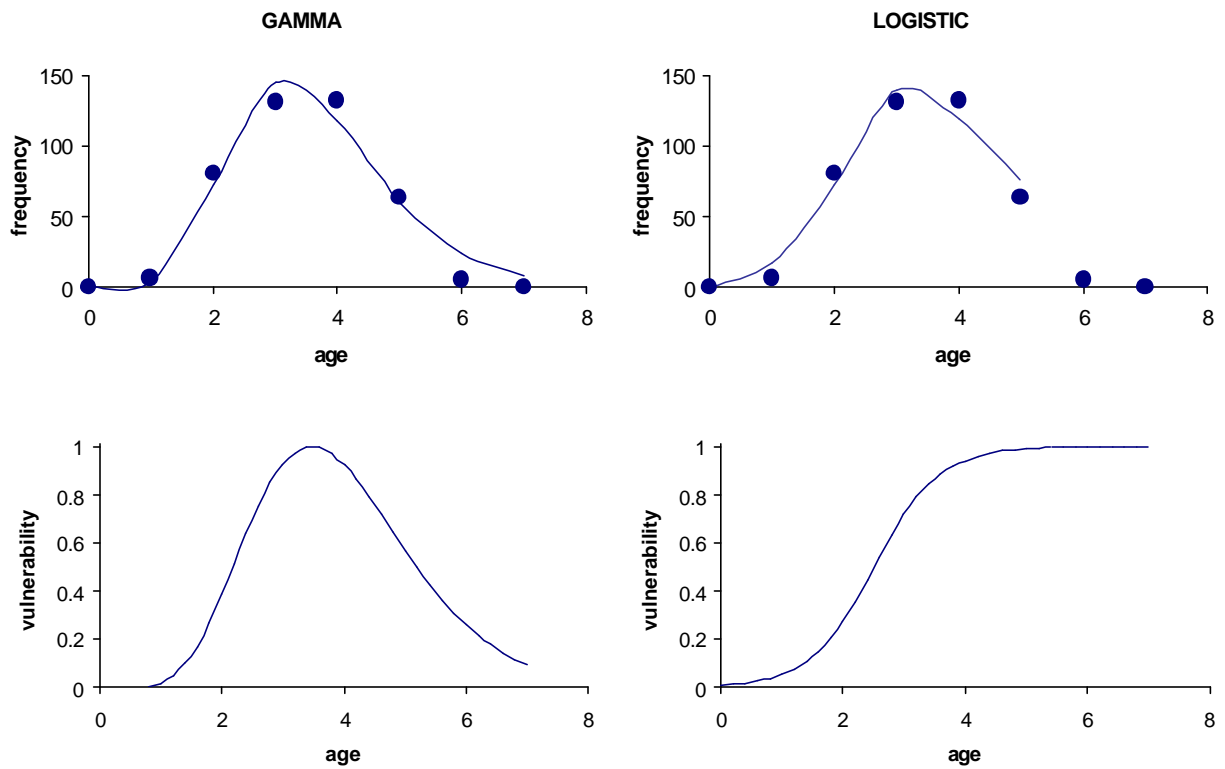


Figure 2. Gamma and logistic vulnerability curves derived by fitting to age-converted length composition data obtained from the Everglades National Park. Top panels show the fit of the expected frequencies at age to the observed values and the bottom panels show the predicted relative vulnerability curves.

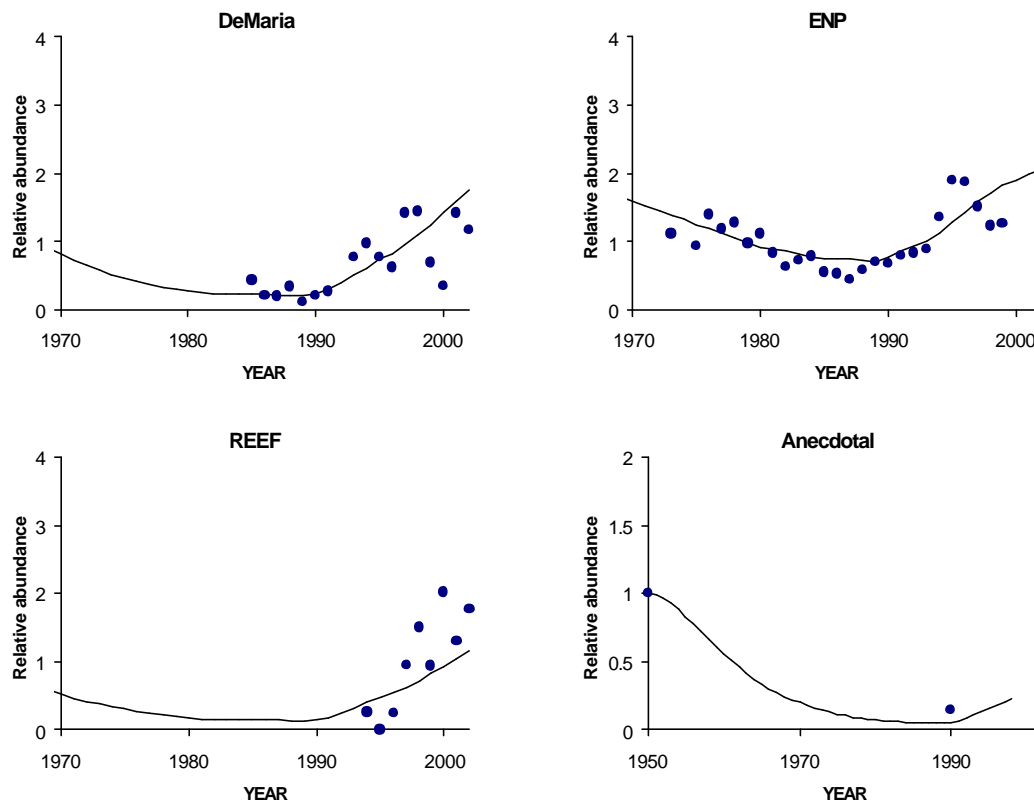


Figure 3. Base model fit to the four indices of abundance.

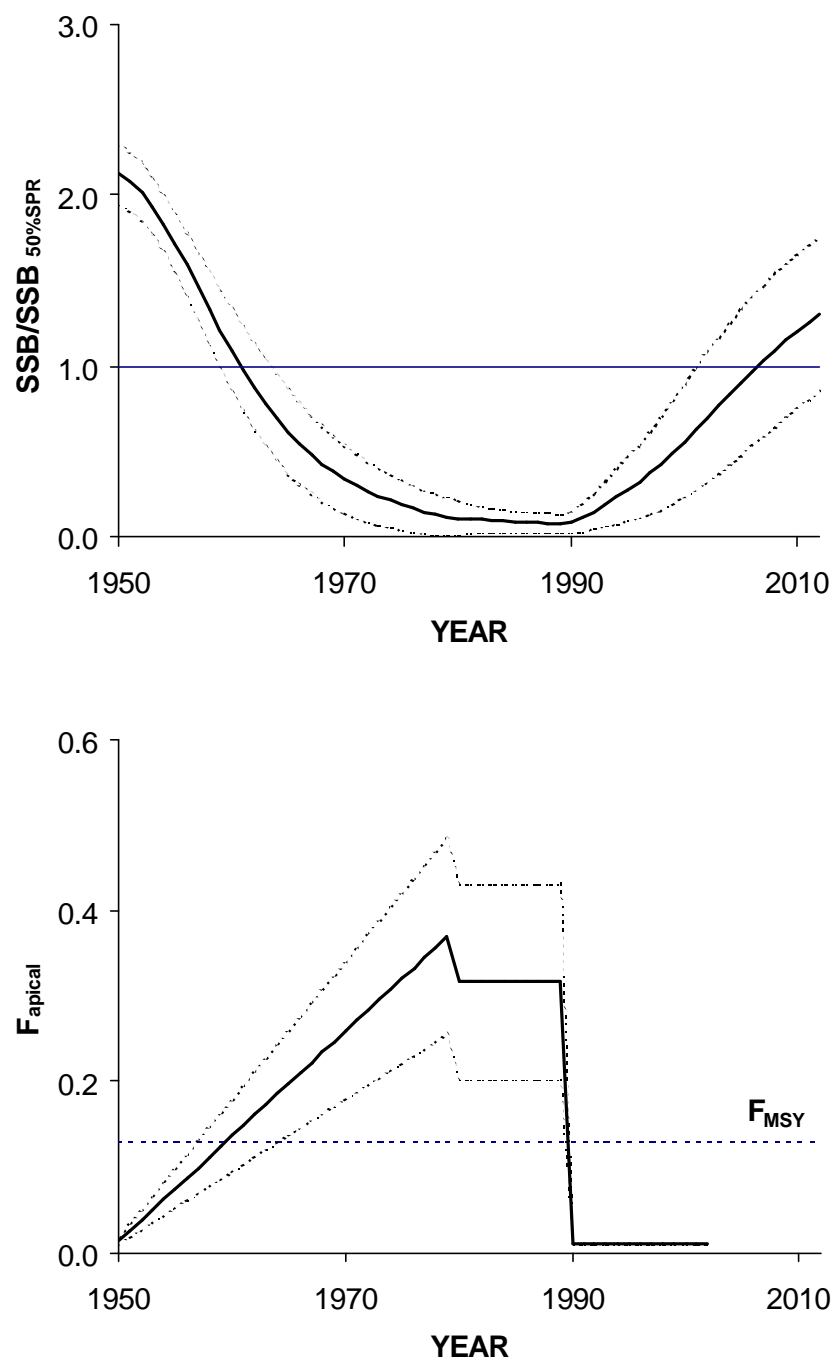


Figure 4. Base model predictions of relative spawning biomass and fishing mortality rate with approximate 80% confidence limits.

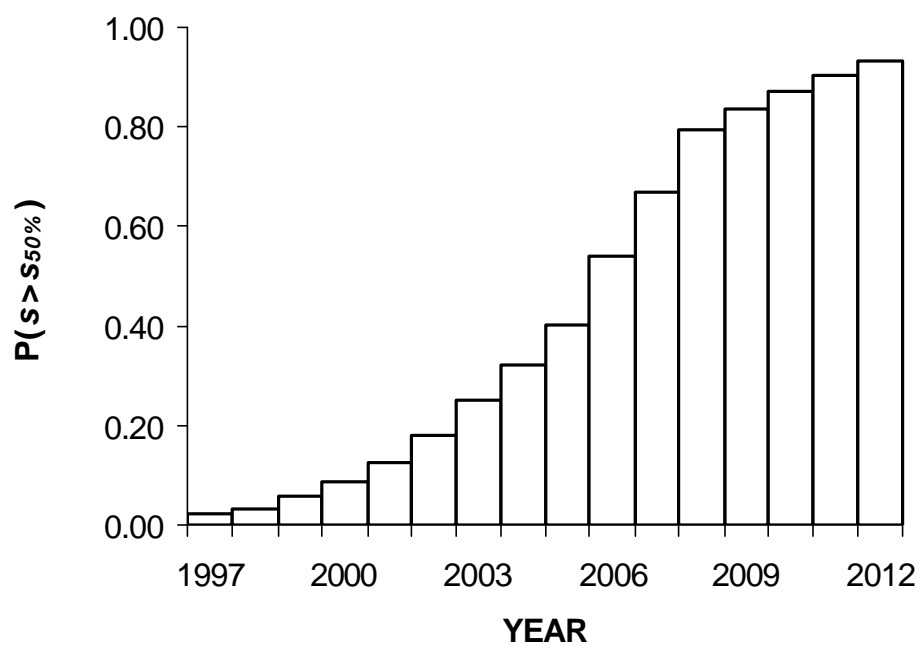


Figure 5. Probability stock will have recovered to spawning biomass levels corresponding to a 50% SPR by year for the base model

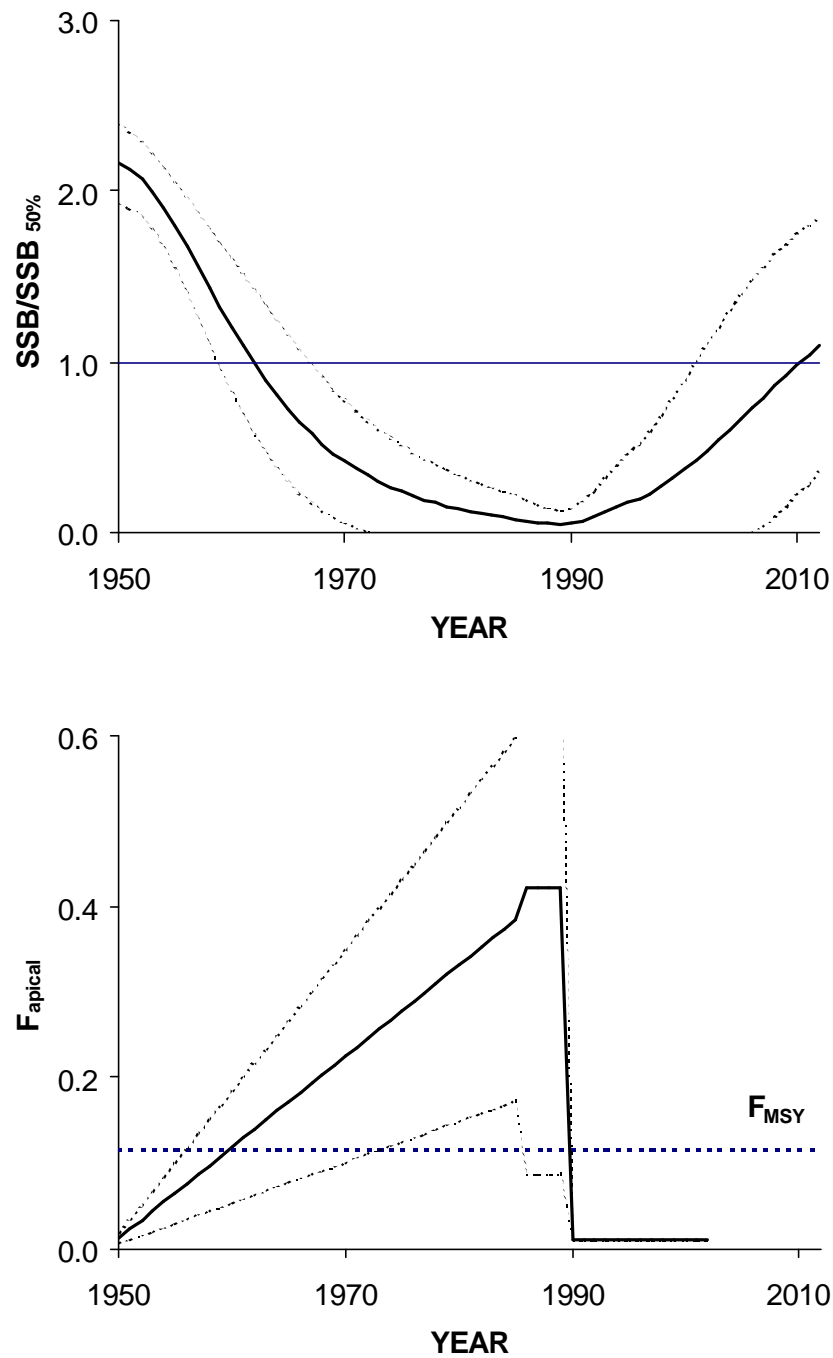


Figure 6. Predictions of relative spawning biomass and fishing mortality rate resulting when base model is applied without the ENP index on juveniles.

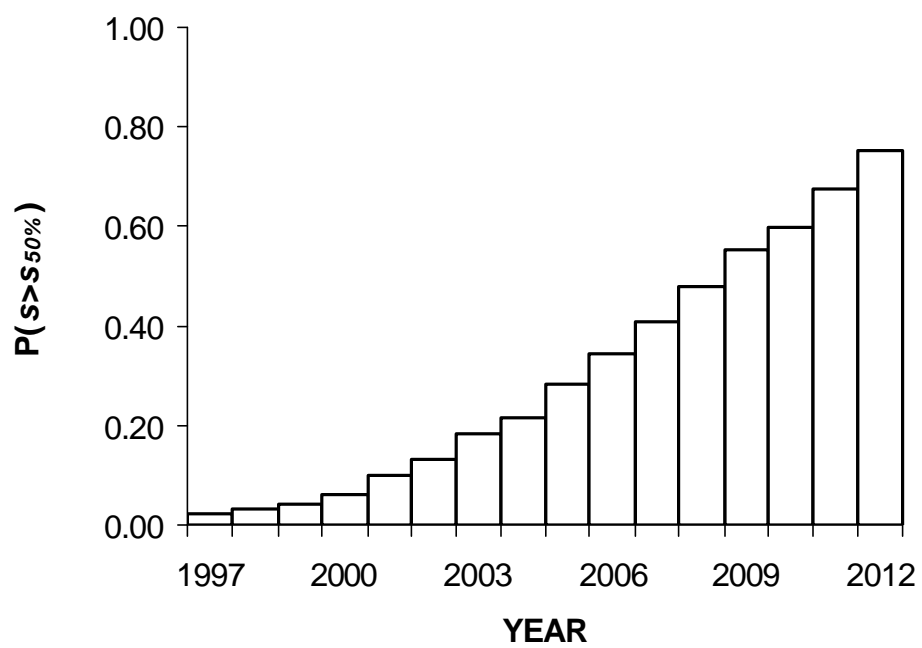


Figure 7. Probability stock will have recovered to spawning biomass levels corresponding to a 50% SPR by year for the base model without the ENP index

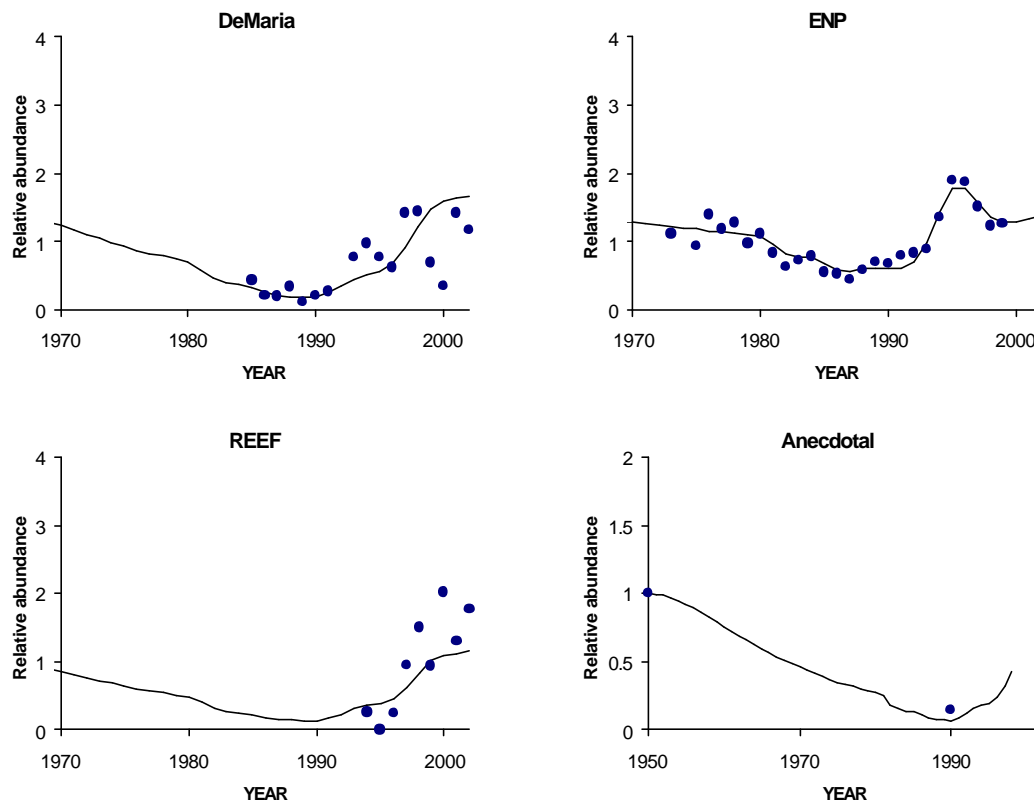


Figure 8. F-deviation model fits to the four indices of abundance.

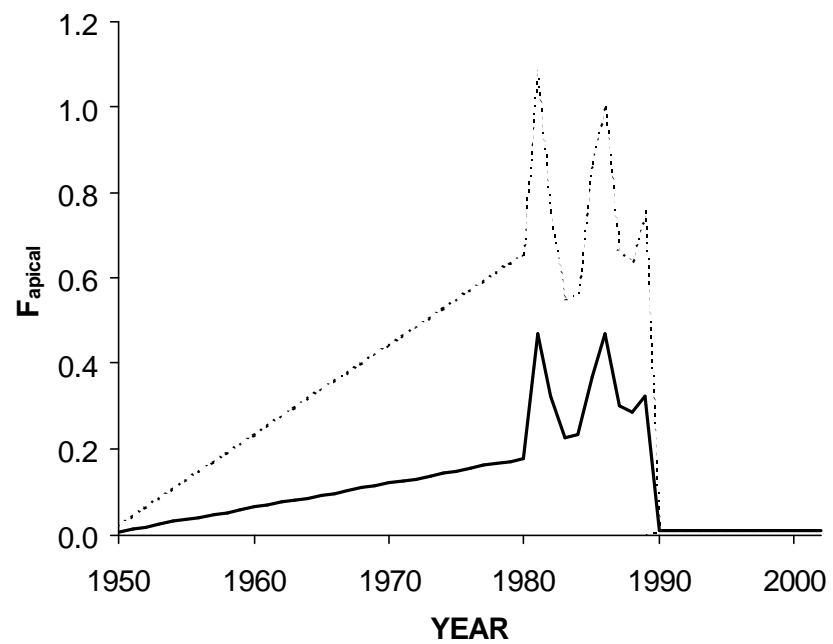
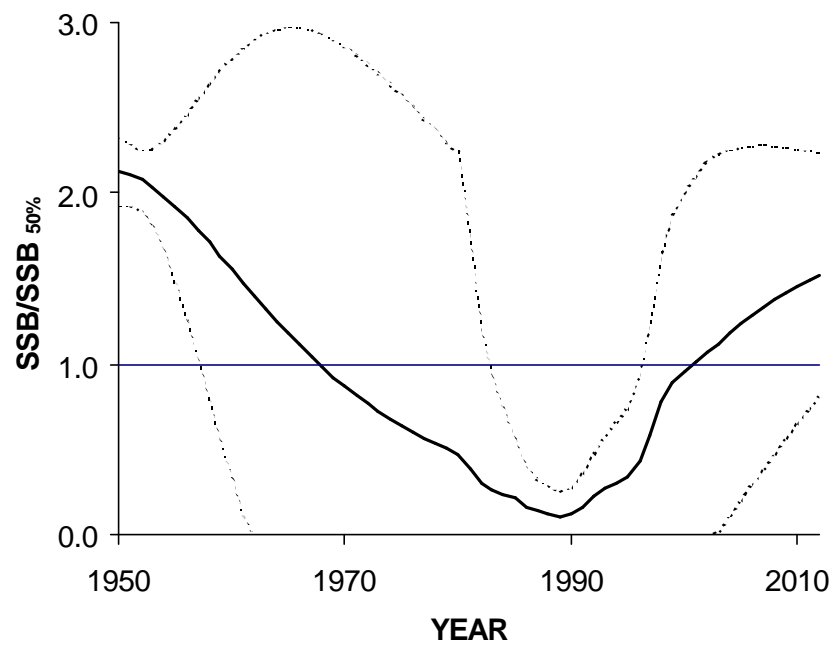


Figure 9. F-deviation model predictions of relative spawning biomass and fishing mortality rate with approximate 80% confidence limits.

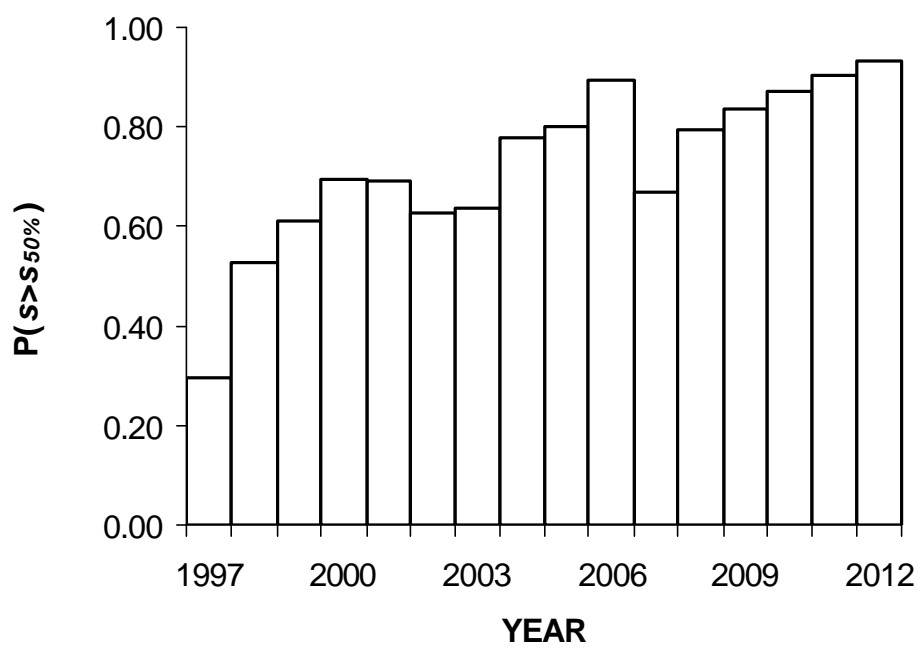


Figure 10. Probability stock will have recovered to spawning biomass levels corresponding to a 50% SPR by year for the F-deviation model